Through the Looking Glass
I. Why Cross-Fertilize?

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24 August 2023

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About

The following pages represent the first volume of a book. The main goal was to introduce the evolutionary problem of sexual reproduction, with a focus on competition between sexual and asexual females. But I also incorporated some ideas on genetic polymorphism and phenotypic plasticity with the goal of exploring "variation strategies" more generally. Finally, I tried to weave in some history of the field, along with some philosophy of science.

Acknowledgements

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Part I

Part One: Why Cross-Fertilize?

Chapter 1

Why Sex?

1.1   The Question

Most PhD programs require that students pass a preliminary examination. This was certainly true in my case. I was a PhD student at the University of Arizona studying rocky intertidal communities in the Northern Gulf of California. But the exams were not focused on our research. They were "depth-of-knowledge" exams. My question from Prof. Astrid Kodric-Brown instructed me to read the preface of G.C. Williams' book, *Sex and Evolution*, which contains the following text (Williams 1975): "This book is written from a conviction that the prevalence of sexual reproduction in higher plants and animals is inconsistent with current evolutionary theory…. Many well informed readers may disagree with much of my reasoning, but I hope to at least convince them that here is a crisis at hand in evolutionary biology….""

The question was something like this: *Why does Williams think that sexual reproduction poses a crisis for evolutionary biology, and what is the solution*? A crisis? That was news to me. How could there be a crisis on evolutionary biology 40-plus years after the modern synthesis? My graduate course in theoretical population genetics did not mention any crises. I was not convinced. And a little freaked out.

The structure of our exams was very loose. I don't remember having a deadline to produce a written answer, but I do remember that I spent several months on just this one question. During much of this time, I was doing field work in Sonora, Mexico, sometimes under very harsh conditions. But the more I studied the question, the more fascinated I became. I came to think that there was, indeed, a very real anomaly presented by sexual reproduction. Williams was right. Perhaps I was especially interested in this anomaly because I had read Thomas Kuhn's "The Structure of Scientific Revolutions" as an undergraduate (Kuhn 1970). Kuhn made the case that dissecting anomalies can lead to interesting advances, and that made sense to me. While I eventually produced an essay to address the question, the answer felt incomplete. I wanted to know more. There were many hypotheses, but there was no clear general explanation. Many years later, I am still working on my prelim question. This book is my revised answer.

1.2   The Problem

There are many problems with sexual reproduction, including the time spent finding mates and the risk of contracting sexually transmitted disease (review in Lehtonen et al. 2012). However, while important, these costs do not form the core of the paradox. Historically, the paradox of sex stems from two things: (1) the cost of meiosis, and (2) the cost of producing males.

1.2.1   The cost of meiosis: reduced relatedness

The "cost of meiosis" was proposed by George Williams (1975). His idea was simply that females are only half as related to their outcrossed offspring as they are to their self-fertilized or parthenogenetic offspring.[1] (See Box 1.1 for condensed definitions.) Williams' idea also had theoretical support, as R.A. Fisher had already shown that an allele causing self-fertilization would rapidly spread to fixation, barring severe inbreeding depression (Fisher 1941). So, why cross-fertilize? The persistence of cross-fertilization despite the cost of meiosis formed a paradox. This paradox created the crisis that Williams saw in evolutionary biology.

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[1]See Bell (1982) for a deeper historical view of the Lottery Model, which involves contributions by Maynard Smith and others, including Williams. I have tried to distill it down to a simple bet-hedging model here. The original formulation is more complex.

1.2.2 The cost of males

The other way to look at the problem was proposed by John Maynard Smith (Maynard Smith 1971, 1978). Here the issue is not relatedness. The problem stems rather from the difference between sexuals and asexuals in their per-capita birth rates (Figure 1.1). Imagine a population of sexual individuals at carrying capacity (K_{sex}). At K_{sex} the sexual females are, by definition, simply replacing themselves. This means that each sexual female is, on average, producing one son and one daughter. Both sons and daughters contribute genetically to the next generation, but only females give birth. Now, consider a mutation in a single female that causes her to reproduce asexually. She gives birth to two daughters instead of one daughter and one son. These two asexually produced daughters both give birth to two more daughters. Hence, after just two generations, the asexual female has four granddaughters, while the average sexual female has just one granddaughter (Figure 1.1). This asymmetry should lead to the rapid replacement of sexual females by asexual females (Figure 1.2.3). And by "rapid," I mean within tens of generations, even for very large populations (Lively 1996). We thus seek a selective force that can give an advantage to sexual reproduction on a very short time scale.

THE COST OF MALES

SEXUAL FEMALE   CLONAL FEMALE
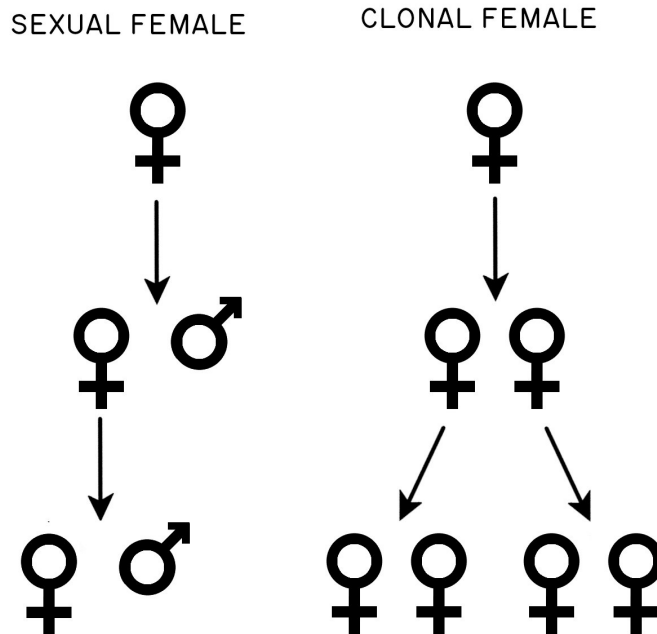
Figure 1.1: The cost of males. Imagine a single clonal female in a sexual population at carrying capacity, K_{sex}. At K_{sex}, the sexual females are, on average, producing one daughter and one son. In contrast, the clonal female produces two daughters and four granddaughters. Hence, the clonal lineage should rapidly eliminate the sexual population (Figure 1.2.3). However, in nature, asexual reproduction is very rare in both plants (Whitton et al. 2008) and animals (Vrijenhoek 1998). Hence the paradox. Why is sexual reproduction so costly and yet so common?

Several assumptions went into Maynard Smith's model for the cost of males. In particular, he assumed that sexual females and asexual females make the same number of offspring, and that the survivorship of these offspring is also the same. Maynard Smith referred to this as the "all-else-equal assumption." Unfortunately, some authors have taken the phrase "all-else-equal" to mean that everything else is exactly equal. But this is not the case. Maynard Smith did not assume, for example, that sexuals and asexuals have the same ploidy value.[2] His model only assumes that sexual and asexual females have equal fecundities and survivorship probabilities (see Box 1.2). Under this assumption, a very rare clone would double in frequency in the next generation. Maynard Smith called this doubling-when-rare the two-fold cost of sex.

1.2.3   Contrasting the costs

The two alternative costs of sex raise an immediate question. Does the cost of sex result from reduced relatedness between mother and offspring, or from the cost of producing males? Or is the cost some combination of both? These questions are not easy to answer; but there is an algebraic solution, which suggests that the (1) two costs are mutually exclusive and (2) that they apply to different kinds of uniparental progeny (Lively and Lloyd 1990). Roughly speaking, I think we can adopt the following rules for the purpose of this book. When considering the spread of a rare allele that induces self-fertilization in hermaphrodites, the appropriate cost is Williams' cost of meiosis. Here we have a single population in which the selfing allele is under positive selection because it has a transmission advantage. On the other hand, when we consider the spread of a clone into an obligately sexual population, we are dealing with competition between two different reproductively isolated groups. One group (the sexuals) produces males, which do not make offspring. The other group (asexuals) produces only females. Here the cost of sex stems from producing males. But the two costs do not combine. The cost of sex is not four-fold.

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[2]The variance in x is equal to the average of the squared deviations from the mean: $var(x) = \frac{1}{N} \sum_{i=1}^{N} (x_i - \overline{x})^2$
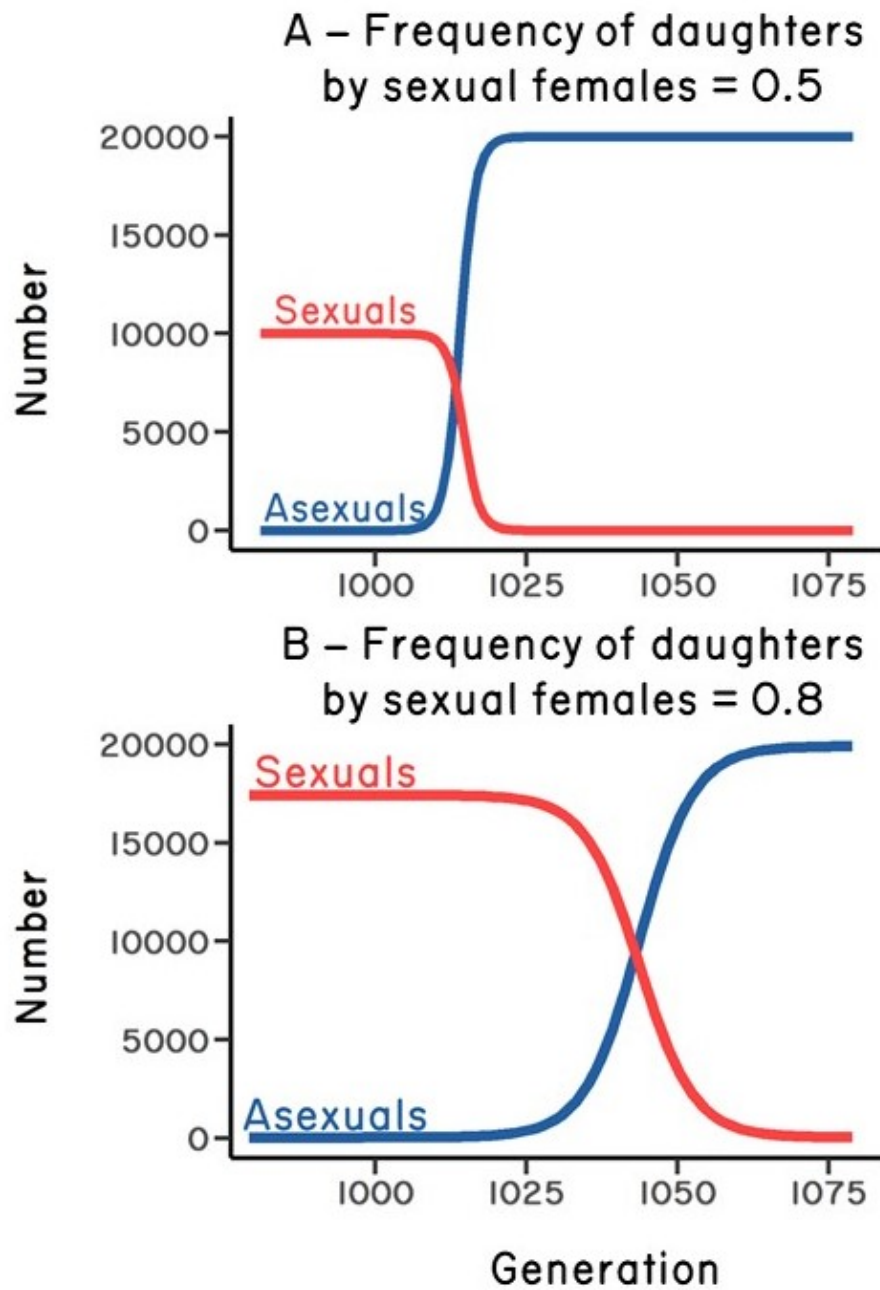
Clonal invasion dynamics. Results from a simulation study in which a single clonal individual was introduced into a sexual population (Lively 2009b). **A** (top). Results for a 1:1 sex ratio in the sexual population. Here the frequency of daughters produced by sexual females was 1/2. The sexual population was

initiated at carrying capacity: $K_{sex} = 10{,}000$. A single parthenogenetic female was introduced by the simulation at generation 1,000. Note that the asexual lineage replaces the sexual population in about 25 generations, and that it reaches a higher carrying capacity $K_{asex} = 20{,}000$. **B** (bottom). Results for a female-biased sexual population. Here the frequency of daughters produced by sexual females was 0.8. The sexual population was initiated at carrying capacity: $K_{sex} = 17{,}500$. As above, a single parthenogenetic female was introduced into the population at generation 1,000. Note that the asexual lineage replaces the sexual population, but it takes longer. The simulation assumes annual reproduction and non-overlapping generations. The R code for the simulation, including interactive graphical output, can be found here. The interactive graph can also be run here for users without R.

1.2.4   The cost of recombination

There is another paradox of sexual reproduction known as the "cost of recombination." Here the competition is not between sexual and asexual females, or between outcrossing and selfing alleles, but rather between alleles that modify the rate of recombination. So instead of asking "Why cross-fertilize?" we can assume cross-fertilization and ask, "Why is there excess crossing-over during meiosis?" Here is the paradox. If combinations of alleles at different loci are favored by natural selection (because together they create high-fitness offspring), then recombination would break these favorable allelic combinations apart. So, it makes no obvious sense to recombine more than needed for normal meiosis. Indeed, Lewontin (1971) formally showed that: *… the mean fitness of the population at equilibrium is a maximum in the absence of recombination.*[3] Hence, there are two interrelated anomalies: cross-fertilization per se and meiotic recombination. Ideally, any theory that explains the persistence of biparental sex could also solve the paradox of recombination. But this need not be the case. They could have different solutions.

💡 Box 1.1

Short definitions of terms as used in this book. These definitions do not include all possible nuances.
Carrying capacity. The population density at which females have just enough food to replace themselves. Sexual females must make two offspring to replace themselves (assuming a 1:1 sex ratio), while asexual females must only produce one offspring. Hence, asexuals should have higher carrying capacities, as shown in (Figure 1.2.3).
Cost of males. The reduction in the per-capita growth rate of sexual populations due to the production of males. The cost of males is the appropriate cost for considering sexual subpopulations in competition with

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[3]The geometric mean is the Nth root of the product of N observations. Compared to the arithmetic mean, the geometric mean gives more weight to small values.

obligately asexual subpopulations.

Cost of meiosis. The reduction in relatedness between mother and off-spring due to outcrossing. The cost of meiosis is the appropriate cost for considering the spread of alleles that induce self-fertilization.

Clone. A lineage of parthenogenetic females descended from the same asexual female. Members of the same clone may have small genetic differences, which accumulate by mutation over time.

Cross-fertilization. The exchange of gametes between different individuals, which may or may not be related.

Outcrossing. A form of cross-fertilization, which specifies crossing between unrelated individuals.

Parthenogenesis. Any form of asexual reproduction through ova.

Recombination. Genetic exchange between homologous chromosomes during meiosis, especially when the exchange leads to gametes with allele combinations not represented on the parental chromosomes.

Self-fertilization. The fusion of gametes from the same individual.

Sex/rec. Shorthand for sexual reproduction and recombination.

Sexual reproduction. I use the term here to mean cross-fertilization between unrelated individuals. However, the term is more general, and can be used to mean the incorporation of novel genetic material by any mechanism.

Hand pollination experiment on *Primula*: a contrivance for cross-fertilization?
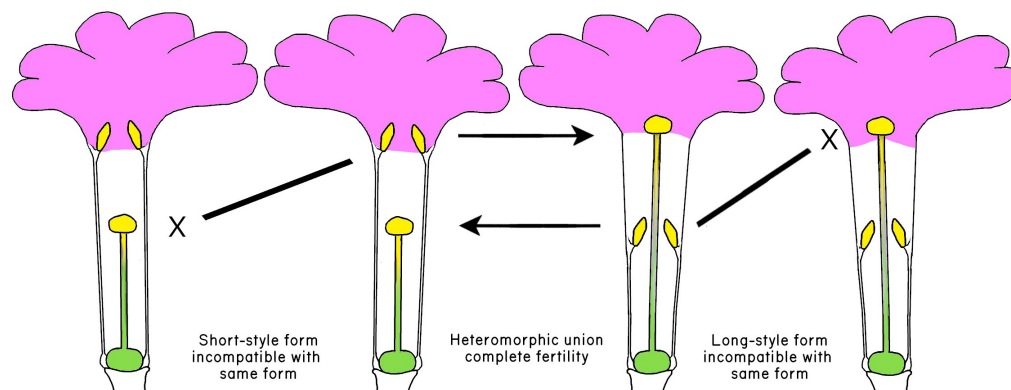
1.2.5 Darwin's view

Even before the cost of males and meiosis were so dramatically revealed by Williams and Maynard Smith, biologists were reckoning with the anomaly of sex (reviews in Meirmans 2009, Dagg 2016). One of the earliest of these biologists was Charles Darwin. After he published the *Origin of Species*, Darwin was

doing hand-pollination experiments at Down House on three species of a curious annual plant in the genus *Primula*. The plant is curious in that it has two morphs. One morph has a style that extends beyond the anthers (the long-style morph), and the other morph has anthers that extend beyond the style (the short-style morph). Botanists refer to this condition as distyly (Figure 1.2). Darwin found that crosses between the different morphs of the same species resulted in a very successful production of seeds, but crosses between unrelated individuals of the same morph were dramatically less successful (Darwin 1862). In discussing these results, Darwin speculated that the two morphs may have evolved to insure cross-fertilization: "Whether or not the dimorphic condition of the *Primula* has any bearing on other points in natural history, it is valuable as showing how nature strives, if I may so express myself, to favour the sexual union of distinct individuals of the same species.""

Darwin then asks a killer question. Why should the union of elements from distinct individuals be favored? Why, in fact, is there sex? "Nor do we know why nature should thus strive after the intercrossing of distinct individuals. We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis. The whole subject is as yet hidden in darkness." Darwin's question shows that the cross-fertilization is curious, even without considering the costs of sex. It also shows how Darwin was drawn to anomalies on theory[4].

It is interesting to note that, in Darwin's quote above, he switches from discussing mechanisms to prevent self-fertilization, such as distyly, to discussing parthenogenesis. Self-fertilization is a sexual process (involving the formation and fusion of gametes from the same parent), while parthenogenesis is an asexual process that does not generally involve meiosis and syngamy (review in Bell 1982). But parthenogenesis and self-fertilization are conceptually related, as they are both uniparental forms of reproduction. Hence, it makes sense that Darwin would switch back and forth between these two different forms of uniparental reproduction. Why cross-fertilize if either selfing or parthenogenesis is an option?

There may be another reason why Darwin pivots to parthenogenesis. Just prior to the publication of Darwin's (1862) paper on *Primula*, Carl Theodor Ernst von Siebold (1856) published his observations on the successful development of adults from unfertilized eggs, which he called "parthenogenesis" (virgin birth). These were revolutionary observations, which caught Darwin's attention. In a letter to his mentor, J.S. Henslow, Darwin mentioned von Siebold's discovery as follows: *There is no greater mystery in the whole world, as it seems to me, than the existence of sexes, – more especially since the discovery of Parthenogenesis.* Letter to J. S. Henslow. See Darwin Correspondence Project.

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[4]The bet-hedging idea dates to Daniel Bernoulli, a mathematical physicist, writing in 1738. Steve Stearns (2000) provides an important, fascinating review of how evolutionary biologists (beginning with Cohen (1966)) and economists, have borrowed from Bernoulli's conceptual framework.

However, the discovery of parthenogenesis[5] was met with some hostility. Consider, for example, the following statement by Rudolf Wagner in his 1857 review of von Siebold's book on parthenogenesis [as translated from the original German by Churchill (1979)]: "I must unfortunately say that one of the most unpleasant of facts, [*Parthenogenesis*] has been introduced into physiology, which for the hope of so-called general laws of animal life-phenomena *is most distasteful.* It is impossible, considering the glorification of our highly vaunted progress in the theoretical understanding of the life processes, for it to be welcomed or particularly encouraged; and sincerely speaking, I can be as little pleased about it as a physicist would be if suddenly one or more exceptions to the law of gravitation were discovered" (Emphasis added).

Clearly, Wagner was not pleased with the discovery of asexual reproduction, calling it unpleasant, unwelcome, and distasteful. By contrast, Darwin did not find the idea to be distasteful in any way. He wondered instead why it was not more common. For example, Darwin (1868) wrote: *Parthenogenesis is no longer wonderful; in fact, the wonder is that it should not oftener occur.*[6]

Over 100 years later, W. D. Hamilton (1975) was also pondering the evolution of outcrossing, and he wrote something conceptually similar: "…complete inbreeding abandons the obviously important advantages of sexual reproduction, whatever these are.""

Whatever these are! The advantages of outcrossing were obviously important because cross-fertilization is so dominant. But the source of these advantages was not clear. At about the same time, Maynard Smith (1976) mused: "One gets the feeling that some essential feature of the situation has been overlooked."

I now think that John Maynard Smith was correct. An essential feature had indeed been overlooked: parasites.

1.3 Summary

1. Obligate sexual reproduction is subject to invasion and replacement by all-female asexual lineages that do not pay the cost of males.
2. Obligate outcrossing in simultaneous hermaphrodites is subject to invasion and replacement by self-fertilization unless inbreeding depression is severe.

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[5]Vrijenhoek studied the coexistence of sexual fish with multiple clonal genotypes of asexual congeners in natural populations. He mainly envisioned the Frozen Niche Hypothesis as a model to explain the coexistence of multiple clones, but it can also explain the coexistence of sexual and asexual modes of reproduction if clonal diversity is low, and the clones do not compete strongly. See, for example pages 112-113 in Vrijenhoek and Parker (2009): "The Frozen Niche-Variation Model (Vrijenhoek 1978, 1979) was directly stimulated by Roughgarden's (1972) ideas and a need to explain the stable coexistence of* Poeciliopsis *fish clones in spatially heterogeneous desert streams (Vrijenhoek 1978)."

[6]Soft selection in theoretical population genetics can also mean that the contribution of offspring from different demes in a metapopulation is unrelated to differences in mean fitness among demes.

3. The exchange of DNA between different parental chromosomes (recombination) is similarly paradoxical.
4. Why then are recombination and cross-fertilization so common?

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i Box 1.2

Maynard Smith's (1978) model showing the cost of producing males.[7]
Let N_{asex} be the number of asexual females at time 1, while N_{sex} gives
the total number of sexual individuals (males plus females) at time 1.
Let B_{asex} give the number of offspring produced by asexual females, and
S_{asex} gives the survival probability of asexual offspring to maturity. The
number of surviving asexual offspring is then $= B_{asex}S_{asex}$. Similarly, let
B_{sex} be the number offspring produced by sexual females, and let S_{sex} give
the survival probability of sexually produced offspring. Maynard Smith
assumed that all individuals reproduce once and then die. Let r be the
frequency of females in the sexual population. The number of asexuals
and sexuals at time 2 can then be calculated as is the table below. (Note,
we do not assume that the population is at carrying capacity).

	Time 1	**Time 2**
N. of asexuals	N_{asex}	$N_{asex}(S_{asex}B_{asex})$
N. of sexuals	N_{sex}	$rN_{sex}(S_{sex}B_{sex})$
Freq. of asexuals	$\frac{N_{asex}}{N_{asex}+N_{sex}}$	$\frac{N_{asex}(S_{asex}B_{asex})}{N_{asex}(S_{asex}B_{asex})+rN_{sex}(S_{sex}B_{sex})}$

The fold increase in frequency of asexuals, F, is the ratio of the frequency of asexuals at time 2 divided by the frequency of asexuals at time 1 giving:

$$F = \frac{N_{asex}(S_{asex}B_{asex})}{N_{asex}(S_{asex}B_{asex}) + r(N_{sex}S_{sex}B_{sex})} \bigg/ \frac{N_{asex}}{N_{asex} + N_{sex}}$$

Under the all-else-equal assumption, $S_{asex} = S_{sex}$ and $B_{asex} = B_{sex}$, giving:

$$F = \frac{N_{asex}}{N_{asex} + rN_{sex}} \bigg/ \frac{N_{asex}}{N_{asex} + N_{sex}}$$

Assuming that there is a single asexual female at time 1, we get

$$F = \frac{1}{1 + rN_{sex}} \bigg/ \frac{1}{1 + N_{sex}} = \frac{1 + N_{sex}}{1 + rN_{sex}}$$

If N_{sex} is very large, the solution reduces to $F \approx 1/r$. Hence, the fold increase in the frequency of asexuals, F, is inversely related to the frequency of females (r) in the sexual subpopulation. Assuming a 1:1 sex ratio, $r = 0.5$. Hence, for an equal sex ratio, the increase in asexuals is $\approx$ 2-fold. This result gives the two-fold cost of males. Assuming "all-else-equal" a clone will double when rare when introduced into a large sexual population.

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[7]Wallace (1975) explains that the source of the terms "soft" and "hard" stem from financial discussions of soft currencies vs hard currencies in monetary exchanges. Soft currencies only have value within their home country. In contrast, hard currencies can be exchanged overseas for currencies with similar buying power.

Chapter 2

The Ecological Hypotheses
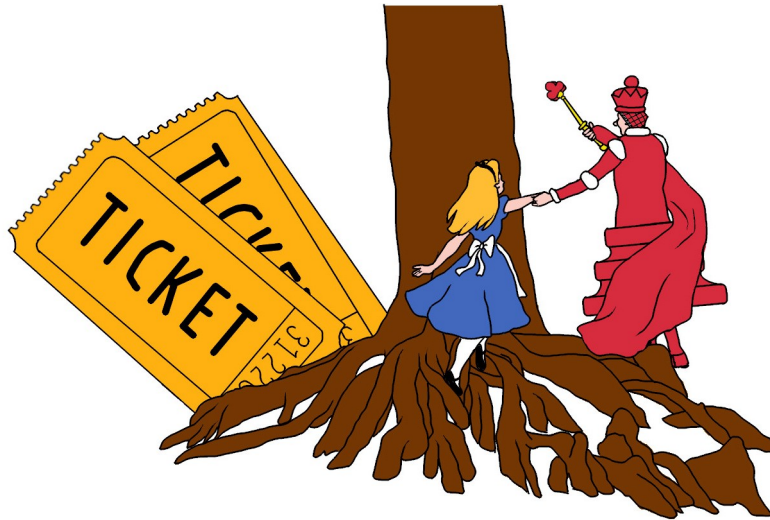
The sex/recombination ("sex/rec") anomaly has attracted some of the best theoretical biologists over the last 50 years, leading to at least two dozen hypotheses to explain selection for recombination and/or the persistence of obligate sexual reproduction in natural populations (Kondrashov 1993). In what follows, I first focus on the ecological hypotheses. The ideas underlying these hypotheses provide a handle for understanding some of the foundational concepts in evolutionary ecology.

2.1   The Lottery Model

As part of his book on the evolution of sex, Williams (1975) suggested that sex could be favored in fluctuating abiotic environments. The idea is intuitive: cross-fertilization generates variation among offspring. Hence, in fluctuating environments, sex could increase the probability that some offspring might survive. Williams likened the idea to a unique kind of lottery. For example, he wrote: "Suppose you were offered this choice in a lottery: either you could have several different tickets, or you could have the same number of copies of the same ticket" (p. 15). If you choose N copies of the same ticket (asex), and your ticket wins, you get N times the reward. If you choose N different tickets (sex), you increase the probability of winning something, but the reward is smaller. Williams referred to the idea as the aphid-rotifer model, but the idea has since come to be known as the Lottery Model (following Bell 1982), which is a more descriptive phrase.[1]

In my evolution course, I ask a form of Williams' question, but with a slight twist:

> If you had a garden, upon which your descendants will depend for many generations to come, would you
>
> 1. plant a genetically variable crop, or
> 2. a monoculture with a two-fold higher yield?
>
> Keep in mind that your descendants will follow your choice.

Often the students rightfully want some clarification. They ask, for example, "Can we use pesticides?" But every time, most students choose the variable crop. I remind them that selecting the variable crop will reduce their yield by one half. They don't budge. I re-ask the question, doubling the relative yield for the monoculture from two-fold to four-fold. Then to 10-fold. Occasionally, one of the more risk-prone students will select the 10-fold higher yield, but most do not budge. They want genetic variation. I ask them why. Invariably, they say that the environment is going to change. They want to hedge their bets against an uncertain future.

Indeed, Williams' Lottery Model is about bet hedging. The gist of bet-hedging in evolutionary theory is that selection can act to reduce the variance in reproductive success over time, even if it also reduces the arithmetic mean across years (review in Philippi and Seger 1989). Suppose, for example, that we have the following data for both a monoculture and a genetically variable polyculture (in arbitrary units). Let's assume that the variation in yield is driven by annual variation in abiotic factors, such as temperature or precipitation. The effect of planting a polyculture (bet-hedging) can be estimated from the geometric mean, which incorporates the variation in yield over time.

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[1] See Bell (1982) for a deeper historical view of the Lottery Model, which involves contributions by Maynard Smith and others, including Williams. I have tried to distill it down to a simple bet-hedging model here. The original formulation is more complex.

Year	Monoculture	Polyculture
1	350	250
2	400	250
3	300	200
4	100	200
5	50	200
Arithmetic mean	**240**	220
Variance[2]	19400	600
Geometric mean (GM)[3]	184	**219**
Approximate GM	200	**219**

In this example, we find that the monoculture has an arithmetic mean of 240, while the polyculture has an arithmetic mean of only 220. So, I might be inclined to plant the monoculture. However, the among-year variance is very high for the monoculture (relative to the polyculture), driven in large part by the low yields in years 4 and 5. By contrast, the geometric mean for the monoculture is 184, while the geometric mean for the polyculture is 219. Based on this, I might be inclined to plant the polyculture, as it reduces the cost of very low yield in bad years. I think the students see this intuitively. Over the long term, it is better to be risk-averse and plant the genetically variable polyculture. What if, for example, the monoculture produced no food in the last year? The geometric mean would be zero. That would be catastrophic.

The effect of variance on the geometric mean (GM) can be seen by an approximation (Stearns 2000):

$$\text{GM} \approx \overline{x} - \frac{\text{var}(x)}{2\overline{x}}$$

where $\overline{x}$ is the mean, and $\text{var}(x)$ is the variance in x. Note that the approximation is equal to the arithmetic mean when the variance in x is zero. Note too that the geometric mean increases as the variance in x decreases. So, if selection operates to reduce the among-year variance in fitness, the outcome of selection will be reflected by an increase in the geometric mean. In general, evolutionary biologists use the geometric mean (rather than the arithmetic mean) to measure fitness over time.[4]

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[2]The variance in x is equal to the average of the squared deviations from the mean: $var(x) = \frac{1}{N} \sum_{i=1}^{N} (x_i - \overline{x})^2$

[3]The geometric mean is the Nth root of the product of N observations. Compared to the arithmetic mean, the geometric mean gives more weight to small values.

[4]The bet-hedging idea dates to Daniel Bernoulli, a mathematical physicist, writing in 1738. Steve Stearns (2000) provides an important, fascinating review of how evolutionary biologists (beginning with Cohen (1966)) and economists, have borrowed from Bernoulli's conceptual framework.

Can sex be favored in variable environments as a bet-hedging strategy? It seems like a very sensible idea, provided that the production of genetically variable progeny reduces the among-year variance in offspring survival. But remember, that under a two-fold cost of sex, asexuals can replace large populations of sexuals in tens of generations (see chapter 1). So, if the Lottery Model is correct, significant environmental change must occur very rapidly. The many thousands of years between ice ages, for example, would be too long.

2.2   The Tangled Bank/Frozen Niche-Variation Model

Roughly speaking, the Lottery Model concerns the value of producing diverse offspring in a temporally variable abiotic environment. A different kind of model instead concerns the role of competition for different resource types that vary in space. Let us first consider the Frozen Niche-Variation Hypothesis of Robert Vrijenhoek. The key idea is that the clonal derivatives of sexual ancestors "freeze" some of the genetic variation in the sexual population. This frozen genotype then determines the resource niche of the clone. It seems reasonable to assume that the niche width of a single clone would be relatively narrow compared to the niche width of the genetically diverse sexual population. So, under this idea, a clone could invade a sexual population, and perhaps displace it from one of its many niches. But a single clone could not completely replace the sexual population (Vrijenhoek 1979). This kind of process could explain those situations in which sexual and asexual females coexist, which was a major advance.[5]

A conceptually similar model was independently developed by Graham Bell: the Tangled Bank Hypothesis (Bell 1982). Bell nabbed the name from the last paragraph of the *Origin of Species*, in which Darwin imagines life as an "entangled bank" of species interacting in a complex network. The core of the idea can be traced back to Howard Levene's (1953) pioneering model, which showed that polymorphism could be maintained in a spatially heterogeneous environment provided that different genotypes specialize on different resources. Levene's model was a major advance, as it showed that genetic diversity could be maintained without heterozygote advantage (Box 2.1). This was also one of the first models to fuse population genetics with ecology. But how does multiple niche polymorphism apply to sex? The idea is that, if selection results in polymorphism, then a genetically diverse sexual population might be resistant to replacement by a clonal lineage that specializes on only one of the available

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[5]Vrijenhoek studied the coexistence of sexual fish with multiple clonal genotypes of asexual congeners in natural populations. He mainly envisioned the Frozen Niche Hypothesis as a model to explain the coexistence of multiple clones, but it can also explain the coexistence of sexual and asexual modes of reproduction if clonal diversity is low, and the clones do not compete strongly. See, for example pages 112-113 in Vrijenhoek and Parker (2009): "The Frozen Niche-Variation Model (Vrijenhoek 1978, 1979) was directly stimulated by Roughgarden's (1972) ideas and a need to explain the stable coexistence of* Poeciliopsis *fish clones in spatially heterogeneous desert streams (Vrijenhoek 1978)."

resource types (as also in the Frozen Niche-Variation Model).

Here is how I pose the Tangled Bank idea to my undergraduate students. I start by giving them a choice between two hypothetical resources, which occur in different parts of the room. One is pizza, the other is broccoli. They all choose pizza. The problem, of course, is that the per-person value of the pizza resource declines as the pizza-eating population grows. At some point, there will be an advantage to specializing on broccoli. This could lead to a polymorphic population composed of obligate pizza eaters and obligate broccoli eaters, where (at equilibrium) the value of both resources is the same. Hence, selection for or against a particular strategy depends on the frequency of that strategy in the population. Perhaps this kind of *frequency-dependent selection* could favor sexual reproduction as a way to diversify offspring in environments where different resource types are patchily distributed in space. This reasoning forms the essence of the Tangled Bank Hypothesis.

One especially interesting aspect of the Tangled Bank Model is that the strength of frequency-dependent selection depends on population density. For example, there would be no selection to utilize the resource of lower value (broccoli) if there were no competition for pizza. This kind of selection, where the advantage to being rare depends on population density, is sometimes referred to as "soft" selection (Wallace 1975).[6] In other words, soft selection is selection that is both frequency-dependent and density-dependent. This idea contrasts nicely with the Lottery Model, where selection is both frequency- and density-independent, which is called "hard" selection. For our purposes, we can use Wallace's terminology to conceptually separate the Tangled Bank Hypothesis from the Lottery Model Figure 2.1.

We can think of the contrast like this. Under the Lottery Model, changes in the environment will select against certain genotypes independent of whether they are common or rare. Selection seems unconditional (hard). Under the Tangled Bank, selection is always conditional (soft); there is an advantage to having a rare genotype, but this advantage only accrues under strong competition (high density). Soft selection may not be exactly the best possible phrase, but it contrasts nicely with hard selection.[7]

Two caveats are worth mentioning with respect to soft selection and the Tangled Bank Hypothesis. One is that polymorphism is only stable under a narrow range of patch-types frequencies. In addition, strong tradeoffs are required for the cost and benefits for morphs occupying different patches (Maynard Smith and Hoekstra 1980, Lively 1986a) (see also Box 3.1). The second caveat is that

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[6]Soft selection in theoretical population genetics can also mean that the contribution of offspring from different demes in a metapopulation is unrelated to differences in mean fitness among demes.

[7]Wallace (1975) explains that the source of the terms "soft" and "hard" stem from financial discussions of soft currencies vs hard currencies in monetary exchanges. Soft currencies only have value within their home country. In contrast, hard currencies can be exchanged overseas for currencies with similar buying power.

Figure 2.1: Partitioning the ecological hypotheses for the maintenance of obligate sexual reproduction. The figure is redrawn from Wallace (1975). The inserted blue text shows how the ecological hypotheses fit into Wallace's matrix for density-dependent selection vs frequency-dependent selection. The Lottery Model relies on hard selection in temporally variable environments. The Tangled Bank relies on soft selection in spatially variable environments. The Red Queen relies on frequency-dependent selection generated by coevolving antagonistic species.

	DENSITY	
	INDEPENDENT	**DEPENDENT**
FREQUENCY — INDEPENDENT	HARD SELECTION Lottery Model	DENSITY-DEPENDENT SELECTION
FREQUENCY — DEPENDENT	FREQUENCY-DEPENDENT SELECTION Red Queen	SOFT SELECTION Tangled Bank

repeated mutation to asexual reproduction could lead to the accumulation of clonal diversity over time. Once all the niches are occupied by different specialized clones, there would be no advantage to sex. A diverse clonal population could then replace the sexual population (Bell 1982, Vrijenhoek and Parker 2009). This second caveat applies, in general, to any model of sex that relies on frequency-dependent selection. But the ideas could work if mutations to asex are rare. And, as I mentioned, sexuals and asexuals are known to coexist in some populations, which is consistent with the Tangled Bank and Frozen Niche-Variation Hypotheses (Vrijenhoek and Parker 2009). Coexistence, however, is also compatible with the Red Queen hypothesis, which we will now consider.

2.3 The Red Queen Hypothesis

The Red Queen Hypothesis is like the Lottery Model in that it focusses on environmental change over time. However, under the Red Queen idea, the change is mediated by changes in coevolving biological antagonists such as parasites, rather than changes in the abiotic environments.[8] The distinction is important, as we will see.

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[8]I use "parasite" here in the ecological sense to include any organism that lives in, or on, its host, provided it reduces the survivorship and/or fecundity of its host. As such, the term includes both macroparasites (such as worms) and microparasites (such as protozoans, bacteria, and viruses).

It may be helpful to revisit Figure 1.2.3, which shows the replacement of a sexual population by a clonal lineage within 25 generations. In this example, the clone was a single genotype, while the sexual population was composed of multiple recombining genotypes, only one of which was shared with the clone. Clearly, as the clone spreads, its genotype would become the most common in the host population. Now suppose that the host population is coevolving with a parasite population, which is composed of multiple strains. Assuming random contact between hosts and parasites, the parasite strain that could infect the most common host genotype would have a selective advantage over parasite strains that could only infect rare host genotypes. Let's call this more successful parasite strain "strain **A**." What would happen? It should be easy to see that strain **A** would increase in frequency. The parasite population would evolve.

Now, what if the parasite dramatically reduces the reproductive success of infected hosts? We might expect that, as the parasite evolves to infect the most-common host genotype, the reproductive advantage of the host clone is eroded. Moreover, if the parasite is *common and sufficiently virulent*, evolution by the parasite could prevent the clone from eliminating the sexual population. Under this scenario, there are at least two possible outcomes. One is that the sexuals and asexuals come to exist in stable frequencies, where the lost fecundity of the clone due to infection is equal to the cost of males, meaning that the mean fitnesses of sexuals and asexuals are equal. On the other hand, if the parasite is highly virulent, the frequencies of sexuals and asexuals can oscillate over time (Figure 2.2 A). Under this second scenario, the new clone initially increases, but it is driven down sharply by infection (Figure 2.2 B). Then, once the clone becomes very rare, it should become less infected than observed in the sexual population (Figure 2.2 B). During this period, there is parasite-mediated selection against sex. Hence, the clone increases in frequency (Figure 2.2 A), only to be driven down again by parasites after it becomes common (Figure 2.2 B). Another cycle begins. **The key point is that parasites do not select against clonal reproduction per se; they only select against common genotypes.** But selection against common host genotypes might be sufficient to prevent fixation of a clone in the short term.

This scenario of fluctuating selection for and against sex is just a special case of the more general idea that parasites will select against common genotypes within a diverse, sexual host population. As a rare host genotype becomes common, the parasites genotype that can infect it will be favored by natural selection. If the parasite is virulent (meaning that infection reduces host fitness), the targeted host genotype will decline in frequency, and a new host genotype will begin to increase in frequency. Under this logic, host-parasite coevolution will lead to the oscillation of genotypes in both the host and the parasite populations (Figure 2.3). These oscillations are now called Red Queen dynamics. Red Queen dynamics can lead to the maintenance of genetic polymorphism in sexual populations, and possibly protect sexual reproduction from replacement by asexual lineages. In addition, Red Queen dynamics could also favor recombination within a sexual population (Peters and Lively 1999, Schmid-Hempel and

Figure 2.2:   Simulation model
showing that coevolving parasites
can prevent the fixation of asexu-
als in the short term. **A.** The num-
ber of sexual and asexual individ-
uals over time. **B.** The frequency
of infection in sexual and asexual
individuals over time. The sim-
ulation introduces a single clonal
genotype into a sexual popula-
tion at carrying capacity. After
the clone becomes common (**A**)
the parasites evolve to "target" it
for infection (**B**). Note that af-
ter the parasites have driven the
clone's frequency down, the asex-
uals are less infected than the sex-
uals. Simulation model based on
Lively (2009), which treats para-
site virulence as a positive func-
tion of host density.
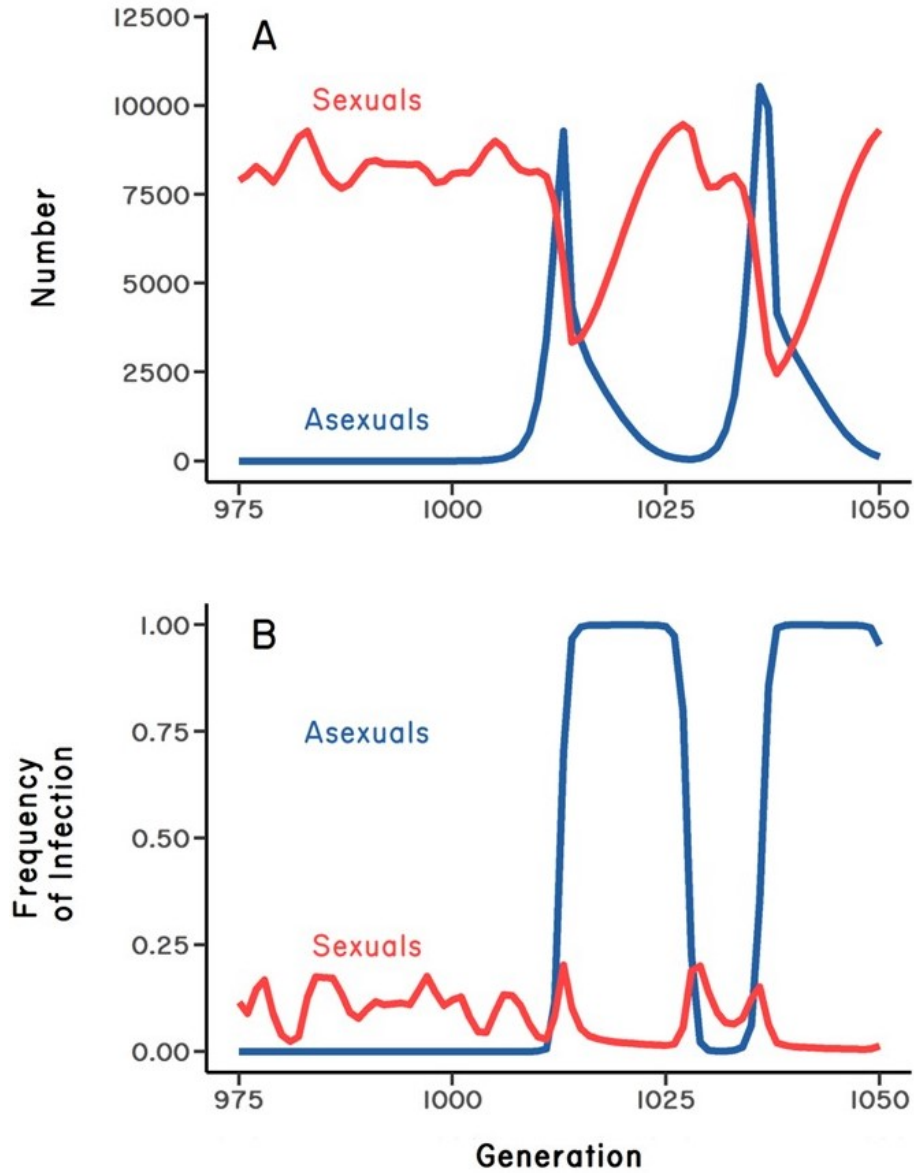
Jokela 2002, Peters and Lively 2007, Salathe et al. 2008). These related ideas are now called the Red Queen Hypothesis (following Bell 1982).
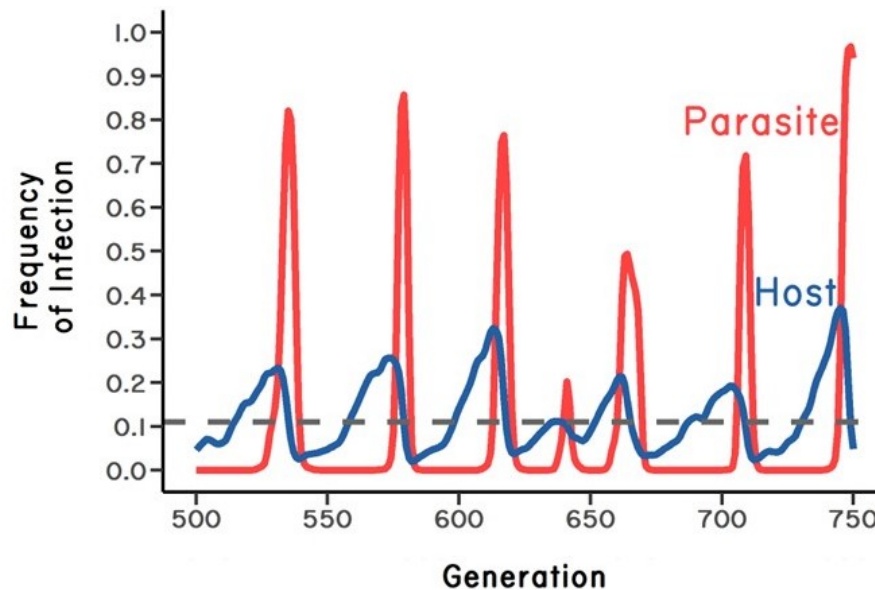

Figure 2.3: Red Queen dynamics. The frequency of a single host genotype is shown along with the frequency of the only parasite genotype that can infect it. Note that the parasite tracks the host with a time lag. Results were extracted from a simulation of a sexual host population with nine possible genotypes coevolving with an asexual parasite with nine matching genotypes Lively (2009). The dashed line shows the average genotype frequency for hosts and parasites.

2.3.1 An intersection of science and literature

The name for the Red Queen Hypothesis comes from *Through the Looking Glass* (Carroll 1872). Here are the relevant bits of the story. After Alice goes through the looking glass (a mirror), she decides to follow a straight path to the top of a hill. But, in following the path, she ends up at her starting point. Talking to herself, she remarks, "But how curiously it twists! It's more like a corkscrew than a path." Repeated attempts were unsuccessful. In frustration, Alice addresses a tiger lily amongst a patch of flowers, "I wish you could talk!" The lily informs Alice that all the flowers can talk. The stunned Alice then begins a conversation with the flowers before finally asking, *Are there more people in the garden besides me?* The rose answers *yes, there is someone like you.* Alice sets out to follow this person (the Red Queen), but she quickly loses sight of her, and ends up back at her original starting point. Flustered, Alice decides to follow the advice of the rose: "I should advise you to walk the other way." Alice then quickly finds the Red Queen.

Now it gets especially interesting. Alice mentions to the Red Queen that she would like to "find my way to the top of the hill." The Red Queen replies: "I could show you hills in comparison with which you'd call that a valley." Alice protests: "a hill ca'n't be a valley… That would be nonsense." This exchange between Alice and the Red Queen now seems prophetic, because, under frequency-dependent selection, locations on the adaptive landscape can rapidly change from fitness peaks to fitness valleys. Perhaps the Red Queen's state-

ment is correct: hills can become valleys, and valleys can become hills. More specifically, genotypes that were favored by natural selection when rare can become selected against after they become common, leading to a highly dynamic adaptive landscape.

In any case, Alice had clearly entered a crazy world. Straight paths become like corkscrews, progress is made by going the other way, and hills become valleys. Then, suddenly, Alice and the Red Queen began to run: "Alice never could quite make out, in thinking afterwards, how it was that they began: all she remembers is, that they were running hand in hand, and the Queen went so fast that it was all she could do to keep up with her." During this furious run, Alice notices that they never pass anything. The trees remain in the same place as if they were moving along with them. Alice eventually asks: "Are we nearly there?" The Red Queen replies: "Why, we passed it ten minutes ago! Faster!"

When they finally stop, Alice is surprised to be where they started: "I do believe we have been under this tree the whole time! Everything is just as it was!" The Red Queen replies that of course, and then asks: "What would you have it?" Alice replies that she would have expected to get somewhere else after running for a long time. The Red Queen then replies with this very famous quote: "Now, *here*, you see, it takes all the running *you* can do to keep in the same place." It is a perfect metaphor for host-parasite coevolution[9]. Host and parasite genotypes might oscillate as if they were running to stay in the same place.

It seems unlikely that Lewis Carroll had coevolution in mind when writing these passages. But he was a mathematician at Oxford University (his given name was Charles Dodgson), and at least one author has shown how his writings can be seen as metaphors for mathematical problems (Bayley 2009, 2010). Along these lines, mathematician Sanderson M. Smith has suggested that Carroll simply inverted the equation for speed from "speed = distance/time" to "speed = time/distance". Upon rearrangement, the latter gives "distance = time/speed." Hence you must run very fast to stay in the same place. But how does the shifting landscape fit in? And why did Alice have to go the other way to meet the Red Queen? I would love to know.

It is perhaps worth pointing out that the phrase "Red Queen Hypothesis" can have two different meanings to evolutionary biologists. In the early 1970s, Leigh van Valen was grappling with data showing that the probability of extinction in very different organisms was independent of the age of the lineage. He reasoned that, in coevolutionary interactions, the probability of one species driving the other species extinct could, in fact, be independent of lineage age (Van Valen 1973). It thus seems reasonable to suggest that both antagonists must run (coevolve) as fast as they can to prevent extinction. Graham Bell repurposed the phrase to mean within-population oscillations in host and parasite

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[9]The intersection between science and literature is not restricted to selection for or against sex. For a fascinating essay on how the biology of parasites meets literature, see Justyna Jajszczok's dissertation (Jajszczok 2017).

genotypes (Bell 1982). Hence, Van Valen's idea is about macroevolution (speciation/extinction), while Bell's idea is about microevolution. Even though van Valen's use of the Red Queen metaphor was published first, I will use Bell's microevolutionary meaning, as it perfectly captures the oscillating nature of genotype frequencies during host-parasite coevolution.[10]

2.3.2 Conceptual roots of the Red Queen Hypothesis

Part of my goal is to show science as a process. As such it seems reasonable to discuss the origins of the Red Queen idea. One of the earliest statements alluding to the Red Queen Hypothesis came from W.D. Hamilton (1975). Hamilton was reviewing the books by Williams (1975) and Ghiselin (1974) for the *Quarterly Review of Biology*. Throughout the review, the reader can feel Hamilton's frustration with their arguments. Towards the end, he makes this very abstract suggestion: "…it seems to me that we need environmental fluctuations around a trend line of change" and "For the source of these we may look to fluctuations and periodicities … generated by life itself."

The quote does not specifically refer to parasites, but it does suggest that coevolutionary interactions, in general, could play a role in selecting for sex and recombination. In his memoirs, Hamilton clears this up, writing: "At that stage when I wrote the review, although I had not seen the particular relevance that parasitism might have, I had for many years seen sex looming ahead and had reached a stage of being excited by the possible primary role of biotic interaction. I had decided that it was in aspects of the interspecies struggle, and not survival in an inanimate environment, that I had to search for the main factor. Adaptation to new physical habitats might be made possible through sexuality but these adaptations could not be the main reason for its existence (Hamilton 2001)."

Note that, here, Hamilton is specifically contrasting host-parasite coevolution with the Lottery Model, which relies on random changes in "physical habitats."

At about the same time, a plant population biologist, Don Levin, was also writing on the paradox of sex/rec. In his paper, Levin specifically identified pathogens as a possible force selecting for recombination (Levin 1975): "I propose that the persistent tracking of plant hosts by multiple pathogens and herbivores is a prime factor which prohibits the congealing of the genomes of species, especially those in closed communities."

Boom! By "prohibit the congealing of genomes," Levin means, "selects for recombination." The reference to "closed communities" means species that are tightly coevolving in the absence of homogenizing gene flow. This quote seems

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[10]I. M. Lerner used the Red Queen metaphor as early as 1954, with respect to the selection needed to maintain genetic homeostasis: "The *Alice in Wonderland* situation in which 'it takes all the running you can do to stay in the same place' arises when a stationary level of performance can be maintained only by application of the maximum selection possible…" (See page 117 in Lerner (1954)).

to be the first to specifically identify coevolving pathogens as a primary source of selection favoring the mixing of genomes. Levin's idea was quickly followed by important conceptual contributions by Glesener & Tilman (1978)[11], Jaenike (1978)[12], and Lloyd (1980). In particular, Lloyd writes: "… biological interactions are more likely than unpredictable physical conditions to provide the kind of relentless, repetitive change that is necessary for sexual parents to be selected because of the genetic diversity that sex engenders."

Lloyd then turns this abstract idea into a specific prediction, which I would later test: "If this proves to be so, we will then be able to examine whether the occurrence of asexual reproduction is correlated with relaxation of the biological hostility of the environment." Notice that, in the quotes presented above, both Hamilton and Lloyd were specifically predicting that coevolution is more important in selecting for sex than uncertain physical environments. But it is reasonable to ask, does it really matter? Aren't both ideas fundamentally about bet hedging in uncertain environments? Yes: I think both ideas are about bet hedging. But the distinction still matters. The Lottery Model is about random shifts in the direction of selection; there is no selection against common genotypes unless the environment changes by chance in a way that disfavors them. By contrast, under the Red Queen, selection is frequency dependent. In fact, selection against common genotypes is the core of the model. Hence, the critical difference between the models is not so much about bet hedging but whether selection for sex/rec is directional (but randomly changing directions, a lottery) or frequency dependent (Red Queen). For example, parasites could be a source of directional selection for sex if they randomly changed which host genotypes they attacked. To my mind, that would be a Lottery Model. The Red Queen Hypothesis requires frequency-dependent selection generated by interactions between species.[13] This is an important distinction.

Taking this view, the Red Queen Hypothesis may seem more closely related to the Tangled Bank model than to the Lottery Model, as both the Red Queen and the Tangled Bank rely on frequency-dependent selection. But the critical distinction here is that selection against common genotypes under the Tangled Bank relies on intraspecific competition in populations at carrying capacity (soft selection). The Red Queen relies on interspecific antagonistic coevolution, leading to parasite-mediated selection against common host genotypes.[14]

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[11]For example, Glesener and Tilman write: "Thus, sexuality not only is favored under changed conditions but is, itself, capable of changing the conditions. The sexuality of an organism's competitors, predators, parasites, etc., will greatly increase the selective pressure for sexuality on that organism as well."

[12]Jaenike focuses more on the recycling of genotypes: "My hypothesis differs from Levin's in that sex and recombination are advantageous not to produce novel genotypes as such, but to produce rare genotypes, of which novel ones are only a subset."

[13]I use "frequency-dependent" selection here to mean selection against common genotypes. A more accurate phrase would be "negative frequency-dependent" selection.

[14]This is not meant to imply, however, that the strength of parasite-mediated selection under the Red Queen Hypothesis must be independent of population size. Indeed, as we will see, there are good reasons to think that the strength of parasite-mediated selection depends on

In any case, looking back, it seems clear that the architects of the ecological hypotheses had two inter-related things in mind:

1. How can we explain sex/rec, and
2. How do we understand the biogeographic and phylogenetic distributions of asexual reproduction?

As an evolutionary ecologist, I was drawn to the confluence of these questions. But other ideas were also interesting, such as the idea that sexual reproduction is favored because it reduces the interference between alleles at different loci (review in Otto 2021). I will cover some special cases of this latter idea in Chapter 3.[15]

2.4 Summary

1. Three ecological hypotheses have been proposed to explain the persistence of cross-fertilization in the face of competition with uniparental reproductive strategies such as parthenogenesis or self-fertilization (following Bell 1982).

2. The Lottery Model is based on the possible advantages of diversifying offspring facing uncertain changes in the abiotic environment. Here selection is independent of both density and frequency.

3. The Tangled Bank and Frozen Niche-Variation Hypotheses are based on competition for resources when multiple resource types co-occur. Selection is frequency dependent, but the advantage to rare types only occurs when intraspecific competition is intense.

4. The Red Queen Hypothesis relies on parasite-mediated selection against common host genotypes. Such selection, when strong, can result in oscillatory changes in parasite and host alleles. These oscillations are sometimes called Red Queen dynamics.

5. A bet-hedging strategy reduces the variance in reproductive success over time, even if it reduces the arithmetic mean. Sexual reproduction under the Lottery Model is clearly a bet-hedging strategy. The Red Queen idea can perhaps also be seen as bet hedging.

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host density.

[15]The basic idea comes from a paper by Hill and Robertson (1966), and is often called the Hill-Robertson effect (following Felsenstein 1974). A broader framework, housed under the more intuitive phrase "selective interference," was recently given by Sarah Otto as part of a keynote lecture given to the American Genetic Association (Otto 2021).

> **i** Box 2.1. Levene's model of multiple niche polymorphism.
>
> It was widely thought that heterozygote advantage was required to maintain polymorphism at a single locus with two alleles. In the introduction to his paper, Levene wonders "...whether it was in fact possible to have an equilibrium without the heterozygote being superior in any single niche." The paper is not easy to follow, even though the algebra is not difficult. Here I try to simplify the presentation.
> Levene first assumes that the proportion of survivors coming from the ith niche is constant (q), independent of the genotypic composition of the niche (i.e., soft selection). He then assumes that the heterozygote has a relative fitness of 1 in all niches, giving $W_{AB} = 1$. Let q be the frequency of allele A, and let $(1-q)$ be the frequency of allele B. The frequency of allele A in the next generation, q', is then
>
> $$q' = \sum c_i \frac{q^2 W_{AAi} + q(1-q)}{q^2 W_{AAi} + 2q(1-q) + (1-q)^2 W_{BBi}}$$
>
> The change in q is simply $q = q' - q$. Under these assumptions, Levene showed that A allele will increase when rare (barring genetic drift) when |
>
> $$\frac{1}{\sum c_i \frac{1}{W_{AAi}}} < 1$$
>
> where the left-hand side gives the harmonic mean fitness for genotype AA over all niches. The right-hand-side of the equation gives the harmonic mean fitness of the heterozygous genotype, AB, which is equal to 1. Similarly, the B allele will increase when rare when
>
> $$\frac{1}{\sum c_i \frac{1}{W_{BBi}}} < 1$$
>
> where the left-hand side gives the harmonic mean fitness for genotype BB over all niches. A genetic polymorphism is expected if both alleles can increase when rare, hence **polymorphism is expected when, in general, when the harmonic mean fitness for the heterozygote is greater than the harmonic mean fitness for either homozygote**. But does this require that the AB genotype is the most fit in at least one niche? Levene gives a specific example to answer this question. He assumes two niches, where the proportion of survivors from both niches is equal (i.e., $c_1 = c_2 = 0.5$). He then assumes genotypic fitness values, as given in the following table. It is important to note that the heterozygous genotype is not the most fit genotype in either niche.

	Fitness Niche 1	Fitness Niche 2	Arithmetic mean	Harmonic mean
Genotype				
AA	$W_{AA1} = 1.50$	$W_{AA2} = 0.67$	1.09	0.93
AB	$W_{AB1} = 1.00$	$W_{AB2} = 1.00$	1.00	1.00
BB	$W_{BB1} = 0.67$	$W_{BB2} = 1.50$	1.09	0.93

For this example, the harmonic mean fitness for the heterozygote is greater than the harmonic mean fitness for either homozygote, thus meeting the conditions given by the equations above. Thus, the answer to Levene's question is yes. It is possible to have a genetic polymorphism without having heterozygote advantage in any single niche. And, interestingly, the polymorphism is expected even though the arithmetic mean fitness of the heterozygote is less than the arithmetic mean fitness of either homozygote. Finally, based on this example, it seems that a trade-off is required, such that the AA genotype does best in one niche, and the BB genotype does best in the other niche.

Nonetheless, Levene's result suggests that overdominance for harmonic mean fitness is required for multiple niche polymorphism (Prout 1968). However, Timothy Prout showed that a polymorphism could be stable, even if one allele is dominate, thus ruling out any kind of overdominance (Prout 1968). Let both the AA and AB genotypes have a fitness of 1 in both niches. Let the BB genotype have a fitness of 0.5 in niche 1 and a fitness of 1.67 in niche 2. Assuming as above that both patches are equally common, we get the following table.

	Fitness Niche 1	Fitness Niche 2	Arithmetic mean	Harmonic mean
Genotype				
AA	$W_{AA1} = 1.00$	$W_{AA2} = 1.00$	1.00	1.00
AB	$W_{AB1} = 1.00$	$W_{AB2} = 1.00$	1.00	1.00
BB	$W_{BB1} = 0.50$	$W_{BB2} = 1.67$	1.09	0.77

Prout showed that there would be a stable multiple niche polymorphism, even under complete dominance, provided that the arithmetic mean fitness for BB is greater than 1, and that the harmonic mean fitness for the BB genotype is less than 1. So, clearly, overdominance for harmonic mean fitness is not required for a stable polymorphism.

The papers by Levene (1953) and Prout (1968) helped to lay the foundation for the fusion of population genetics and population ecology.[16]

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[16]The harmonic mean is not intuitive to most Biology students. So, I ask them this question: if you had a score of 100 on your first exam, and a score of 60 on your second exam, would you rather have your final grade calculated as the arithmetic mean or the harmonic mean of the two scores? After some thought, they all pick the arithmetic mean.

Figure 2.4: Plot showing Δq as a function of q for Prout's model of dominance. Note that Δq is positive when q is near zero, and that Δq is negative when q is near 1. There is an interior equilibrium near $q = 0.5$.
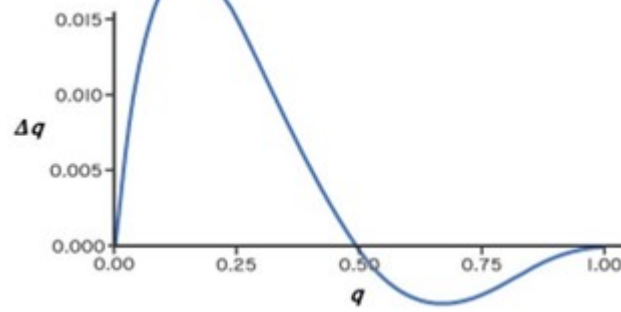
Chapter 3

The Ratchet and the Red Queen

In 1988, Indiana University advertised for an assistant professor in population biology, with emphasis on disease ecology. Lynda and I both applied. Happily, we were offered a split position in Biology in which we each got half salary. It may not sound like a good deal, but we were thrilled. It is not easy for a dual-career couple in the same field. We relocated to Bloomington in January of 1990, arriving during a cold snap (-20&degC). We moved into a university house; but we did not know enough to have the electricity turned on before arrival. Luckily, we still had our down sleeping bags, which we had purchased for field work in the Southern Alps. Aside from the chilly start, moving to Bloomington was the beginning of an academic dream come true. Most of this book aims to highlight the work of my incredible students and colleagues at IU.

3.1 The Problem

Part II

Back Matter

References